

RANUNCULUS GLACIALIS SUBSP. ALASKENSIS SUBSP. NOV. (RANUNCULACEAE),  
A BERINGIAN RACE OF AN OTHERWISE ATLANTIC SPECIES

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ABSTRACT

**Ranunculus glacialis** subsp. **alaskensis** is described as a new Beringian subspecies of an otherwise amphi-Atlantic and European species.

KEY WORDS: Alaska, *Ranunculus*

RESUMEN

Se describe **Ranunculus glacialis** subsp. **alaskensis** como una nueva subespecie Beringiana de una especie anfiatlántica y europea.

The Seward Peninsula of western Alaska provides the closest geographic connection between North America and Northeast Asia across the Bering Strait where the continents are separated by less than 100 km. It has been of biogeographic interest since the early work of Eric Hultén who, in his classic 1937 study, developed the concept Beringia as a periglacial refugium for plants, involving both Asia and America. A.E. Porsild, also a prominent figure for his extensive early fieldwork, provided floristic details and described several new species (1939) from western Alaska. Yurtzev (1972), Murray et al. 1994, and Ickert-Bond et al. (2009) have summarized the floristic patterns of the Beringian flora to highlight what is similar on both sides of the Bering Strait and what is very different.

Intensive floristic inventories of the region were initiated in the 1980s by Kelso (1983, 1989). These continued through collaborative U.S.–Russia teams organized by the Panarctic Flora Project and sponsored by the National Park Service Beringian program in 1992 and 1993. In 1996 and 1997, as part of rare plant surveys supported by the U.S. Geological Survey, remote areas were investigated with helicopter support. Field work has brought about the discovery of taxa new to the region, to North America, and three taxa new to science: *Primula anvilensis* (Kelso 1987), *Douglasia beringensis* (Kelso et al. 1994), and *Parrya nauruaq* (Al-Shehbaz et al. 2007).

A previously unknown *Ranunculus* was found at four localities, all in the Kigluaik Mountains (Fig. 1) on the central Seward Peninsula. Persistent white petals that become reddish in age and the persistent sepals with dark reddish-brown pubescence are features shared with the amphi-Beringian *R. camissonis* Schltldl. and the amphi-Atlantic *R. glacialis* L.

Löve and Löve (1956) and several subsequent authors assigned *R. glacialis* and *R. camissonis* to the genus *Beckwithia* Jeps. [*Erythraea* 6:97 (1898)], together with the type species *Beckwithia andersonii* (A. Gray) Jeps. [*Ranunculus andersonii* A. Gray], an endemic of western U.S.A.: CA, OR, ID, NV, UT and AZ. Whittemore (1997) kept these three species within *Ranunculus* but assigned them to *Ranunculus* sect. *Crymodes* (A. Gray)

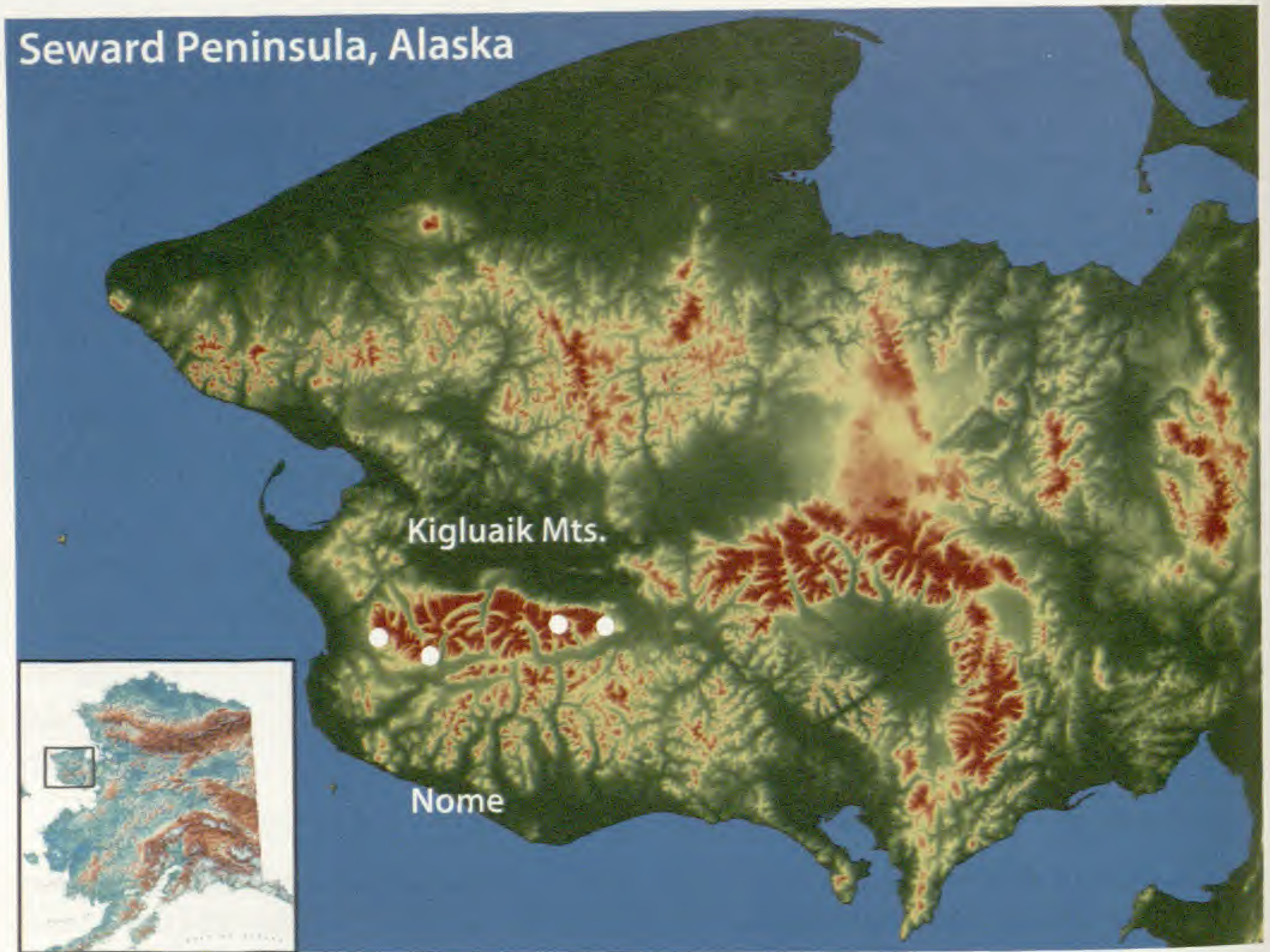


FIG. 1. Map showing distribution of *Ranunculus glacialis* subsp. *alaskensis*.

A. Gray, also based on *R. andersonii*. The morphological and molecular analyses of Hörandl et al. (2005), Paun et al. (2005), and Emadzade et al. (2010), using sequences of the *matK/trnK* and *psbJ-petA* regions, support *Beckwithia* as a genus apart from *Ranunculus*, but monotypic, consisting only of *B. andersonii*.

The two northern species of *Ranunculus*—*glacialis* and *camissonis*—have been allied with European species of sect. *Aconitifolii* Tutin containing the tall-grown and white-flowered *R. aconitifolius* L. and *R. platanifolius* L., which are confined to montane and subalpine tall-herb communities, and with *R. seguieri* Vill. and *R. kuepferi* Greuter & Burdet, alpine species of scree slopes and margins of snowbeds, respectively. The northern taxa, *R. glacialis* and *R. camissonis*, have a contrasting history, ecology, and distribution, but studies by Paun et al. (2005) show that the species of section *Aconitifolii* are phylogenetically coherent.

*Ranunculus glacialis* and *R. camissonis* have the following characteristics in common: Perennial plants with most leaves basal, long-petiolate, with blades deeply trisected or ternately divided (with more or less petiolulate leaflets in *R. glacialis*), main segments mostly dissected anew; flowering stems one to several with 2–4 leaves, similar to the basal ones or less divided, and with 1–3 (4) flowers; lower parts of the plant subglabrous or glabrous, upper parts with peduncles and sepals more or less densely pubescent with dark golden-brown hairs; petals 5–8, broadly obovate, white, becoming red-tinged and then purple after pollination. Both species are diploids with  $2n = 16$ . We recognize three taxa: two species, *R. camissonis* and *R. glacialis*, the latter with two infraspecific taxa subsp. *glacialis* and subsp. *alaskensis*. Subspecies *alaskensis* is new to science.

## KEY TO THE TAXA

1. Stems mostly single, erect; blades of radical leaves deeply dissected into three oblanceolate to nearly linear main segments, often divided anew, with obliquely upward pointing subacute lobes, the two lateral main segments often smaller than the central one, blades cuneate at base; flowers single; sepals ovate; peduncles and sepals densely hairy \_\_\_\_\_ *R. camissonis*
1. Stems mostly several, ascending; blades of radical leaves ternately divided, main segments reniform in outline, subdivided into short, obtuse to rounded lobes, not upward pointing, the two lateral main segments nearly the same size as the central one, blades broadly cuneate to more or less truncate at base; flowers 1–3(–4); sepals obovate \_\_\_\_\_ *R. glacialis*
2. Stems and peduncles glabrous (in the Alps with light, loosely appressed pubescence on peduncles); sepals with flexuose hairs up to 2 mm long, mostly appressed \_\_\_\_\_ subsp. *glacialis*
2. Stems and especially peduncles with dense, long hairs; sepals with hairs 2–4 mm long, spreading to descending \_\_\_\_\_ subsp. *alaskensis*

***Ranunculus glacialis* L.**

*Beckwithia glacialis* (L.) Å. Löve & D. Löve

In our concept, this is a European, amphi-Atlantic, and American Beringian species with two subspecies, the ranges of which are reported below. It is found in wet to damp gravelly or stony habitats, in open vegetation directly on mineral substrates without peat or other soil profiles, often in high alpine and arctic snowbank environments, on gravel bars along brooks and rivers, in periglacial environments including fresh morainal gravel and nunataks, and in wet or north-facing humid screes.

***Ranunculus glacialis* subsp. *glacialis***

The range is amphi-Atlantic. It is found in eastern Greenland, Jan Mayen, the southernmost part of Svalbard, Iceland, Fennoscandia eastwards to the Khibiny Mountains on the central Kola Peninsula (Russia), and in the major central European mountain ranges from the Pyrenees eastwards to the Carpathians. It reaches the altitudinal limit among vascular plants in Scandinavia (2370 m.s.m. Lid and Lid 2005) and is among those plants reaching the highest elevations in the Alps.

***Ranunculus glacialis* subsp. *alaskensis* Yurtzev, subsp. nov. (Fig. 2).** TYPE: U.S.A. ALASKA: Seward Peninsula, Kigluaik Mountains, W of Glacial Lake, ca. 700 m.s.m., stony barrens and rubble screes, 11 Jul 1993, D.F. Murray, B.A. Yurtzev, T. Kelso 11398 (HOLOTYPE: ALA; ISOTYPE: LE).

A forma typica caulibus in partibus superioribus et pedunculis atrorufae pubescentibus (nec glabris vel subglabris), sepalorum pilis saepius ad 4 mm longis, patentibus, rectis (non saepius subadpressis, brevioribus, flexuosis) differt. A *Ranunculus camissonis* foliis circumscriptione reniformibus (nec cuneatis), ternatis (foliolis petiolulatis), segmentis numerosibus, pro more obtusiusculis, latioribus brevioribusque (nec anguste lanceolatis, subacutis), caulibus ascendentibus vel rarius subprostratis (non suberectis vel erectis, gracilibusque) differt.

Habitat in peninsula Sewardensi Alaskae Occidentalis in montibus kigluaikensibus in decliviis et summatibus lapidosis glareosisque (non calcareis).

Subspecies *alaskensis* differs from subsp. *glacialis* by having in the upper parts of stem and peduncles dark brownish-red pubescence (not glabrous or subglabrous as in subsp. *glacialis*), sepals with hairs up to 4 mm long, patent, erect to descending (vs hairs subappressed, shorter and flexuose). It differs from *R. camissonis* in its blades reniform in outline (not cuneate), ternately divided with petiolulate main segments, more numerous and more obtuse segments, the lateral ones shorter (not narrowly lanceolate and subacute), stems ascending or rarely prostrate (not suberect or erect), and sepals obovate (not ovate). See Figure 2.

This subspecies is known only from western Alaska: Seward Peninsula, four sites in the Kigluaik Mountains (Fig. 1) on rocky slopes of platy scree and on ridges and summits on non-calcareous substrates.

***Ranunculus camissonis* Schtdl.**

*Ranunculus glacialis* subsp. *camissonis* (Schtdl.) Hultén; *Ranunculus glacialis* var. *camissonis* (Schtdl.) L.D. Benson; *Beckwithia camissonis* (Schtdl.) Tolm.; *Beckwithia glacialis* subsp. *camissonis* (Schtdl.) Å. Löve & D. Löve

This arctic, amphi-Beringian species reaches from the eastern Anyui mountains of northeastern Siberia and northwestern Russian Far East eastwards to western and northern Alaska with outliers in the alpine tundra of boreal mountains in the Interior (cf., Hultén 1968). It is found in moist to wet tundras, often on peat but mostly

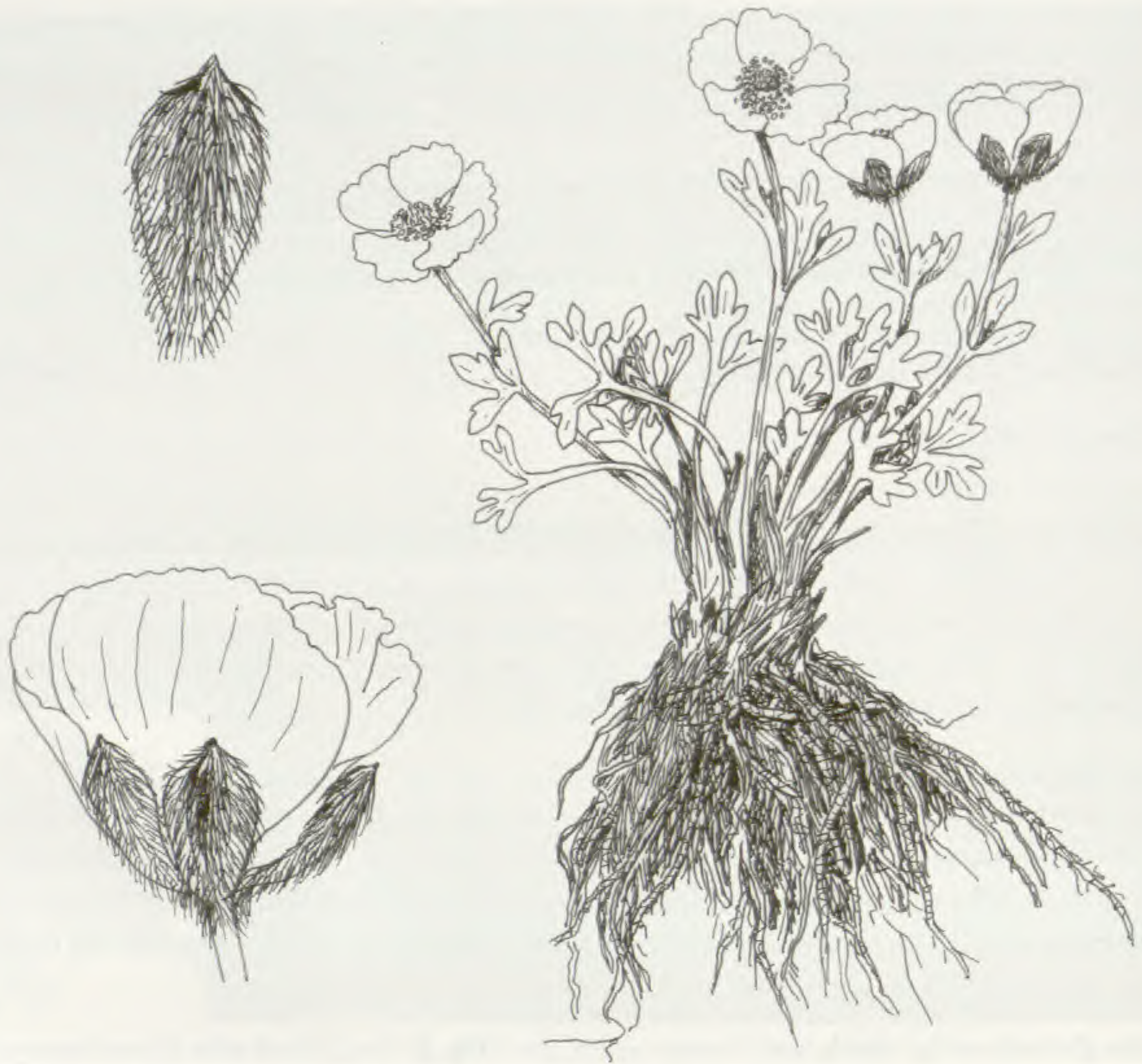


FIG. 2. *Ranunculus glacialis* L. subsp. *alaskensis* Jurtzev, subsp. nov. Habit, flower, and sepal, based on ALA V114478. Alaska: Solomon Quad.: Seward Peninsula, Big Creek Valley, 23 Jul 1993, D.F. Murray, B.A. Yurtzev & T. Kelso 11763. Illustration: Anne Elven.

with underlying calcareous bedrock or morainal material, with a vegetation of forbs, sedges and mosses, often in seepages, in saddles (interfluves), along streams and temporary watercourses, and on moist, non-sorted soil circles ("frost boils"). The species has a preference for circumneutral substrates and avoids both dry limestone and very acidic sites.

*Ranunculus camissonis* differs from *R. glacialis* in several characters. No transitions have been observed in the material studied. Whether this is due to reproductive isolation or to their radically different habitats, making co-occurrence nearly impossible, is not known.

The range of *Ranunculus glacialis* subsp. *alaskensis* is within that of *R. camissonis*. Although the two are in a broad sense sympatric, due to the very different site requirements *R. glacialis* subsp. *alaskensis* is locally allopatric and has not yet been found at or even very close to a site of *R. camissonis*. The two plants are visually quite different, especially in growth shape and leaf shape, and are unlikely, in our view, to be mistaken for each other. Regrettably the illustration provided by Schlechtendal (1819) does not accurately portray the basal leaves of *R. camissonis*. See instead Figure 3 prepared for this paper.

The habitat of subsp. *alaskensis* is very similar to that of Atlantic *R. glacialis* s. str. and quite dissimilar to that of *R. camissonis*. The features it shares with *R. camissonis* are quantitative ones in the amount and length of pubescence and in petal proportions (see Figs. 2 and 3 for sepals). The constellation of characters separating subsp. *alaskensis* from *R. camissonis* and the lack of any transitions is sufficient to justify subsp. *alaskensis* as a taxon separate from *R. camissonis* and belonging to *R. glacialis*.



FIG. 3. *Ranunculus camissonis* Schlttdl. Habit, flower, and sepal, based on ALA V114333. Alaska: Bendeleben Quad.: Seward Peninsula, Minnie Creek headwaters, 16 Jul 1993, D.F. Murray, B.A. Yurtzev & T. Kelso 11597. Illustration: Anne Elven.

Differences between Atlantic and Beringian races of *R. glacialis* are to be expected from the large disjunction, either across the Polar Sea (more than 3000 km) or across nearly the entire continents with gaps of more than 130° longitude from eastern Greenland west to Alaska and more than 150° longitude from Alaska west to the Murman area in European Russia.

Schönswetter et al. (2003, 2004) postulated the persistence of *R. glacialis* in peripheral refugia of the Alps with post-glacial expansion to North Europe by long distance dispersal. However, the disjunctions and the discontinuous morphological variation in *R. glacialis* subsp. *alaskensis* and *R. camissonis* suggest origins well prior to the postglacial period of 10,000–15,000 years ago, although not nearly as early (Miocene) as proposed by Hoffmann et al. (2010). Whereas we agree with an origin in European mountains for *R. glacialis* subsp. *glacialis* or its precursor, we are still unable to offer an explanation for the Beringian *R. glacialis* subsp. *alaskensis* or for *R. camissonis*, which are wholly arctic in distribution.

The Beringian taxa suggest migrations or dispersal events from a European center across to Beringia either by an easterly or westerly direction. Dispersal across Eurasia or North America, without leaving remnant populations is not probable, although that is precisely the explanation offered for similar disjunctions in *Androsace*: dispersal of ancestors or of species from this genus during a warmer interval (interglacial) and subsequent persistence in the Beringian refugium throughout the last glacial maximum with the extirpation of the intervening populations during the full-glacial expansion of glaciers and ice-sheets (Schneeweiss et al. 2004). Fragmentation and significant loss of populations from a formerly more continuous, widely Eurasian or circumpolar range of *R. glacialis* seems unlikely to account for its present limits inasmuch as it has site requirements that are common, widespread, and presumably present continuously, during both glacial and interglacial intervals. How does one account for the remarkable geographic gaps?

A similar case of subspecies with gaps of distribution is *Saxifraga rivularis* subsp. *rivularis* and subsp. *arctolitoralis*, the former European, the latter Beringian with disjunct extensions to Greenland. The two subspecies are explained in this case as two separate, post-glacial, long-distance dispersal events from refugial centers established prior to the last major glaciation (Westergaard et al. 2010).

Any hypothesis as to how *R. glacialis* attained its disjunct range, and subsp. *alaskensis* its characters, is pure guesswork, and the former question may be unanswerable.

A phylogeographic study including *R. camissonis*, *R. glacialis* subsp. *alaskensis* and subsp. *glacialis*, employing plastid DNA and ITS data (Ronikier et al. in prep.), shows that the genetic divergence between *R. glacialis* subsp. *glacialis* on the one hand and *R. camissonis* and *R. glacialis* subsp. *alaskensis* on the other is much more shallow than the genetic split between populations of *R. glacialis* subsp. *glacialis* from the western and eastern Alps, indicating that dispersal to Beringia happened relatively late in the history of the complex. As the Beringian populations are phylogenetically deeply nested in *R. glacialis* subsp. *glacialis* and subsp. *alaskensis* and *R. camissonis* are not readily distinguishable genetically, they prefer to treat *R. camissonis* as subspecies of *R. glacialis* and are reluctant to recognise *R. glacialis* subsp. *alaskensis* as new taxon before better resolution with genetic data becomes available (Schönswetter pers. comm.).

We acknowledge the lack of agreement. Incongruence between phylogenetic and morphological studies of the same taxa are not uncommon. However, we see and by the key demonstrate that there are morphological discontinuities that distinguish the taxa. The fact remains that *R. glacialis* subsp. *alaskensis* has morphological features not found in subsp. *glacialis*. It is possible to discriminate consistently the two subspecies. It follows that the development of these features is under genetic control. It is obvious, too, that subsp. *alaskensis* is distinct from *R. camissonis* and more closely aligned with *R. glacialis*, albeit geographically distant from subsp. *glacialis*. We see no taxonomic value in making the three taxa equivalent. That *R. glacialis* and *R. camissonis* share genetic material is not surprising, but it is not inconsistent to present a taxonomy that emphasizes the sharply contrasting phenotypes and distinct ecological separation between *R. glacialis* subsp. *alaskensis* and *R. camissonis*.

Specimens examined of *Ranunculus glacialis* subsp. *alaskensis*. **U.S.A. ALASKA. Seward Peninsula:** Crete Creek, 64°53'N, 166°08'W, 229–381 m.s.m., 8 Jul 1993, D.F. Murray, B.A. Yurtzev, T. Kelso 11313 (ALA, LE); do., 275 m.s.m., 2 Jul 1996, D.F. Murray, R. Lipkin 12162 (ALA); Glacial Lake, Sinuk River valley, 64°52'N, 165°45'W, 702 m.s.m., 11 Jul 1993, D.F. Murray, B.A. Yurtzev, T. Kelso 11398, holotype (ALA); Big Creek valley, 64°59'N, 164°50'W, 23 Jul 1993, D.F. Murray, B.A. Yurtzev, T. Kelso 11763 (ALA); Upper Fox Creek, 64°59'N, 165°03'W, 914 m.s.m., 5 Jul 1996, D.F. Murray, R. Lipkin 12183 (ALA).

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